Environmental Studies Faculty Publications   Environmental Studies Department

7-2008

Grassland Songbird Survival And Recruitment In Agricultural Landscapes: Implications For Source-Sink Demography

Noah G. Perlut
University of New England, nperlut@une.edu

Allan M. Strong

Therese M. Donovan

Neil J. Buckley

Follow this and additional works at: http://dune.une.edu/env_facpubs

Part of the Environmental Health and Protection Commons, Environmental Indicators and Impact Assessment Commons, Natural Resources and Conservation Commons, and the Natural Resources Management and Policy Commons

GRASSLAND SONGBIRD SURVIVAL AND RECRUITMENT IN AGRICULTURAL LANDSCAPES: IMPLICATIONS FOR SOURCE–SINK DEMOGRAPHY

Noah G. Perlut,[1,5] Allan M. Strong,[2] Therese M. Donovan,[3] and Neil J. Buckley[4]

[1]*Vermont Cooperative Fish and Wildlife Research Unit, The Rubenstein School of Environment and Natural Resources,
81 Carrigan Drive, University of Vermont, Burlington, Vermont 05405 USA*
[2]*The Rubenstein School of Environment and Natural Resources, 81 Carrigan Drive, University of Vermont,
Burlington, Vermont 05405 USA*
[3]*U.S. Geological Survey, Vermont Cooperative Fish and Wildlife Research Unit, The Rubenstein School of Environment and Natural
Resources, 81 Carrigan Drive, University of Vermont, Burlington, Vermont 05405 USA*
[4]*Department of Biological Sciences, State University of New York, Plattsburgh, New York 12901 USA*

Abstract. Population growth and decline are particularly sensitive to changes in three key life-history parameters: annual productivity, juvenile survival, and adult survival. However, for many species these parameters remain unknown. For example, although grassland songbirds are imperiled throughout North America, for this guild, only a small number of studies have assessed these parameters. From 2002 to 2006, in the agricultural landscape of the Champlain Valley of Vermont and New York, USA, we studied Savannah Sparrow (*Passerculus sandwichensis*) and Bobolink (*Dolichonyx oryzivorus*) demography on four grassland treatments: (1) early-hayed fields cut before 11 June and again in early- to mid-July; (2) middle-hayed fields cut once between 21 June and 10 July; (3) late-hayed fields cut after 1 August; and (4) rotationally grazed pastures. We assessed whether these treatments affected adult apparent survival (ϕ) and recruitment (f), how sensitive these parameters were to the presence of nonbreeders and local dispersal, and the populations' ability to persist in these four habitats. On average, birds using late-hayed fields had >25% higher apparent survival than those on the more intensively managed early-hayed, middle-hayed, and grazed fields. Overall male ϕ was 35% higher than female ϕ, and Savannah Sparrow ϕ was 44% higher than Bobolink ϕ. Across all analyses and treatments, apparent survival estimates were 0.58–0.85 for male and 0.48–0.71 for female Savannah Sparrows, and 0.52–0.70 for male and 0.19–0.55 for female Bobolinks. For males of both species, potential nonbreeders decreased the precision of and lowered apparent survival estimates by 25%; female estimates showed little variation with the inclusion of nonbreeders. Inclusion of local dispersal observations increased apparent survival estimates and, in many cases, increased precision, though the effect was stronger for Savannah Sparrows than for Bobolinks, and also stronger for males than for females. High Savannah Sparrow apparent survival rates resulted in stable or near stable populations ($\lambda \approx$ 1), particularly in late-hayed and grazed fields, while low Bobolink apparent survival rates resulted in strongly declining populations ($\lambda < 1$) in all treatments.

Key words: apparent survival; Bobolink; Champlain Valley, New York and Vermont; Dolichonyx oryzivorus; *grassland hayfield management; local dispersal;* Passerculus sandwichensis; *realized lambda; recruitment; rotationally grazed pasture; Savannah Sparrow.*

INTRODUCTION

Population ecology is centered on questions of how and why populations grow and decline. Answers are often found within variations of key demographic parameters, including annual productivity, juvenile survival, and adult survival (Crouse et al. 1987, Donovan et al. 1995, Anders and Marshall 2005). These life-history parameters are difficult to quantify because their estimation is often dependent on individually based, long-term field data. Therefore, demographic

parameters for many species remain unknown. For example, although grassland songbirds are known to be imperiled throughout North America (Peterjohn and Sauer 1999, Murphy 2003, Brennan and Kuvlesky 2005, Sauer et al. 2005), within this guild, only a small number of studies have assessed the individual parameters of annual productivity (Bedard and LaPointe 1985, Bollinger et al. 1990, Kershner et al. 2004*a*, Walk et al. 2004, Perlut et al. 2006), juvenile survival (Wheelwright and Mauck 1998, Kershner et al. 2004*b*, Adams et al. 2006), and adult survival (Bedard and LaPointe 1984, Bollinger and Gavin 1989, Warner and Etter 1989, Perkins et al. 2003, Hagen et al. 2005, Fletcher et al. 2006). Only one study thus far has estimated all of these parameters simultaneously (Fletcher et al. 2006), which allowed

them to examine how sensitivities within these parameters affected population growth.

The need to assess grassland songbirds' life history parameters is particularly important because >70% of the world's remaining grassland habitat is devoted to agriculture and other human use (Hannah et al. 1995). Management intensity of agricultural grasslands has increased recently; for example, farmers harvest hay earlier and more frequently in a season (Troy et al. 2005). However, management intensity varies throughout agricultural landscapes, resulting in a mosaic of management-defined habitats. To date, only annual productivity has been explicitly compared across management types. Results show that annual productivity varies dramatically among management-defined grasslands, where less intensively managed fields have high productivity and are potentially population sources (sensu Pulliam 1988), and more intensively managed fields support little to no productivity and are population sinks (Bollinger et al. 1990, Perlut et al. 2006). Importantly, the strength of these effects varies among species (Perlut et al. 2006). For example, Savannah Sparrow (*Passerculus sandwichensis*) productivity on fields that are harvested early in the breeding season is ~1 offspring per adult female per year, whereas Bobolink (*Dolichonyx oryzivorus*) productivity on those same fields is ~0 offspring per adult female per year. In contrast, both species fledge ~3 young per adult female per year on fields where haying is delayed until after the breeding season (Perlut et al. 2006). Although we are beginning to understand how annual productivity correlates with agricultural management, no study has looked at mortality costs associated with selecting various management-defined habitats within a landscape (but see Bollinger and Gavin [1989] for return rates), and no study has investigated the ability of populations to persist in these habitats.

Survival and recruitment are key parameters in understanding how populations grow or decline. Apparent survival, ϕ, is the probability than an individual survives, returns, and is detected; recruitment, f, is the number of individuals entering a population through birth or immigration per surviving individual already in the population. However, estimation of these parameters is largely dependent on field methodology, which in turn affects inferences about population viability (Pradel 1996, Cooch and White 2007). Two population-level behaviors known to affect parameter estimation are local dispersal (between-year movement off of a study site) and the presence of nonbreeding individuals, floaters, which move on and off a study site without being constrained by parental care at a nest. Inclusion or omission of these behaviors may result in biased parameter estimates. For example, by moderately expanding resight efforts off study sites, ϕ, estimate precision, and the probability of detection can increase significantly (Cilimburg et al. 2002). In contrast, inclusion of nonbreeding individuals can lower apparent survival estimates of breeding populations (Pradel et al. 1997).

To quantify apparent survival and recruitment, the behavioral factors that affect these estimates, and how variation in these parameters affects inferences about population growth, we conducted a demographic study of two obligate grassland songbird species breeding in agricultural grasslands within the Champlain Valley of Vermont and New York, USA. The goal of this study was to address whether four discrete grassland treatments uniquely affected adult apparent survival and recruitment for two songbird species, and to assess how sensitive these estimates are to changes in field methodologies. We (1) estimated apparent survival and recruitment of birds known to be breeding within the boundaries of nine fields that represented the four treatment types that constitute breeding habitat in the Champlain Valley, (2) determined the sensitivity of apparent survival and recruitment estimates to the effects of nonbreeders, (3) determined the sensitivity of apparent survival estimates to effects of local-scale dispersal off the treatment fields, and (4) assessed the finite rate of increase (λ, realized lambda) for each of the four treatment types within the sampling period.

METHODS

Experimental design

We studied four grassland treatment types common in the Champlain Valley: (1) early-hayed fields (EH), hayed between 27 May and 11 June, and generally again in early- to mid-July; (2) middle-hayed fields (MH), hayed between 21 June and 10 July; (3) late-hayed fields (LH), hayed after 1 August; and (4) rotationally grazed pastures (RG), fields in which cows were rotated through a matrix of paddocks and moved after all of the grass in a paddock was eaten to a farm-specific height. Each paddock was thereby given a multiple-week "rest" between grazing events.

We established treatment fields in three study areas: (1) Shelburne, Vermont (2002–2006; EH, LH, RG), (2) Hinesburg, Vermont (2003–2006; EH, LH, MH, RG), and (3) Cumberland Head, New York (2002–2005; LH; 2003–2005; MH). Each treatment field was a minimum of 10.5 ha, and study areas were >8 km apart. Based on landowner and farmer interviews, land use within each study area was consistent for >10 years prior to the initiation of our study. Fields were composed of a mixture of cool-season grasses and forbs (see Perlut et al. 2006 for details on vegetation, management, and study area). In the Champlain Valley, abundances of these two bird species are most strongly affected by landscape characteristics rather than vegetation composition and structure (Shustack 2004) such that the minor differences in vegetation among treatment fields had little effect on bird density.

Field methods

Beginning on 8 May, between 05:00 and 14:00 hours Eastern Daylight Time (EDT), we visited each study field for 1–3 days and deployed 20–24 mist-nets to

TABLE 1. Data sets used (indicated with an x) to examine effects of grassland management of Savannah Sparrow (*Passerculus sandwichensis*) and Bobolink (*Dolichonyx oryzivorus*) apparent survival (φ) and recruitment (*f*) at the study sites in New York (NY) and Vermont (VT), USA.

| Data set | Objective | Parameter | Observations | | | | Study sites |
			On plot	Off plot	Breeders only	Nonbreeders	
Breeders, on plot	1	φ and *f*	x		x		VT and NY
All adults, on plot	2	φ and *f*	x		x	x	VT and NY
Breeders, with dispersers	3	φ	x	x	x		VT
Breeders, no dispersers	3	φ	x		x		VT
All adults, with dispersers	3	φ	x	x	x	x	VT
All adults, no dispersers	3	φ	x		x	x	VT

capture adult birds passively. Once captured, we put unique combinations of three color bands and a single metal U.S. Fish and Wildlife Service band on the legs of all adults of both species. Color-banded birds were continuously resighted throughout the breeding season. In mid-May we began intensive, season-long nest searching and nest monitoring (*n* = 733 Savannah Sparrow nests, and *n* = 447 Bobolink nests). After locating a nest, we immediately identified the associated female and male. If one or both adults were unbanded, we captured and banded those individuals near the nest location. Resight–recapture efforts concluded each year when the last nest fledged or failed (23 July to 23 August). These nest associations provided important resight–recapture data because the breeding status of these individuals was known.

In 2005 and 2006, we supplemented field efforts within the Shelburne and Hinesburg study areas to explore how between-year, local breeding dispersal off study fields affected the sensitivity of adult survival estimates. In 2005 we opportunistically searched all fields within a 1.5 km radius of the three Shelburne treatment fields, one to two times each (including treatment fields, *n* = 57 fields, 457.2 ha). In 2006 we opportunistically searched all fields within a 1.5 km radius of the Shelburne treatment fields one to two times and Hinesburg treatment fields once (including treatment fields, *n* = 257 fields, 1081 ha). Searches occurred on precipitation-free days between 05:00 and 14:00 hours. One or two observers walked through fields swishing 1.5 m bamboo stakes through the grass, flushing birds. We identified each bird as banded or unbanded, recorded its identity, species, and sex, and marked the location of color-banded individuals with a GPS unit. Although singing males were easy to detect and identify, we made a concerted effort to look for and identify less conspicuous females.

From these combined field efforts we created six non-mutually exclusive data sets, consisting of capture–recapture observations (Table 1, sample sizes in Appendix). (1) Objective 1: To quantify φ and *f* for known breeders, we used the "breeders, on plot" data set, including only those individuals on the nine study fields who were socially associated with at least one known nest in any year. (2) Objective 2: To quantify φ and *f* for all breeding and nonbreeding individuals, the "all adults,

on plot" data set consisted of all adults banded on the nine study fields. (3) Objective 3: We used data collected in Vermont to compare estimates of φ across a range of methodologies. For individuals who were socially associated with at least one known nest in any year ("breeders, with dispersers"), we used the seven Vermont study fields, as well as resight data from off-study field searches. "Breeders, no dispersers" included only adults who were socially associated with at least one known nest in any year found only on the seven Vermont study fields. "All adults, with dispersers" consisted of all individuals banded on the seven Vermont study fields, as well as data from off-study field searches. Last, "all adults, no dispersers" included only individuals banded on the seven Vermont study fields.

Analysis methods

Objective 1: Apparent survival and recruitment of known breeders.—We used the Pradel model (Pradel 1996) to assess apparent survival and recruitment in Program MARK (White and Burnham 1999). This analysis focused on survival and recruitment of all individuals who were socially associated with at least one nest in any year and who were marked and resighted within the boundaries of nine study fields (breeders, on plot), to which estimates from Objectives 2 were compared (see next section). Bobolink arrival dates on early-hayed fields complicated this analysis. Because Bobolinks returned to the study sites later in the spring (mid- to late-May) than Savannah Sparrows (late-April to early-May), early haying generally occurred while Bobolinks were in the early courtship or egg-laying stage, disrupting breeding before many nests were identified and breeding status could be ascertained. Bobolinks abandoned early-hayed fields immediately after cutting (Perlut et al. 2006), became nonbreeders, renested elsewhere, or left the Champlain Valley (A. Strong, *unpublished data*). To account for these possible effects caused by the timing of haying, all Bobolinks banded on early-hayed fields before cutting remained in the breeders, on plot set even if they did not have an identified nesting attempt. Finally, breeding observations were made only during nest-monitoring years, therefore breeders, on plot includes NY 2002–2004, all Shelburne fields 2002–2006, and all Hinesburg fields

2003–2005. In non-nest-monitoring years (all NY 2005, and Hinesburg middle- and late-hayed fields 2006), all resighted–recaptured individuals were included in the data set for those specific years.

Our a priori models were developed from data reported in Perlut et al. (2006), where breeding biology varied among the four grassland treatment types, and the magnitude of these effects varied between Savannah Sparrows and Bobolinks. Because the number of successful nesting attempts, the number of clutches laid per female, and response to nest failure (Perlut 2007) varied among treatments, we added sex to the model set to determine if grassland management affected males and females differently. Therefore, with treatment, species, and sex as explanatory variables of ϕ and f, the candidate model set included all combinations of two-way additive, two-way interactive, and three-way additive models for both ϕ and f ($n = 50$ models). Our data could not support a three-way interactive model. Finally, because management was consistent within a given field over the course of the study, we treated ϕ and f as constant across all years. Although environmental variation may also have minor effects on ϕ and f, we believe that management consistency overshadowed these effects.

The resight probability, P, potentially varied among years and sites because nest searching efforts resulted in greater time spent on a given field as compared to non-nest searching years, and field crew sizes and experience varied between the New York and Vermont sites. To account for this variability, p was modeled as a function of state (NY vs. VT) and nest search effort (nest search vs. no nest search) for all Objective 1 models.

We used an information-theoretic approach (Burnham and Anderson 2002) to compare and rank alternative models, and model averaged to obtain overall apparent survival and recruitment estimates for each treatment, species, and sex. We obtained model averaged parameter estimates (ϕ and f) and 95% confidence intervals by summing the products of the estimates and their AIC_c weight (ω_i) for all models. We determined the relative importance of each factor (treatment, species, sex) by summing the products of the survival and recruitment estimates and their AIC_c weight (ω_i) for the top models which accounted for >99% of model AIC_c weights. Parameter estimates are presented with standard error (± 1 SE). Confidence intervals for the β coefficients that did not include zero were considered biologically significant. The coefficients within our linear models indicate the strength and direction of the effect for each of the model factors relative to the reference factor. The reference factors for treatment, species, and sex were late-hayed fields, Savannah Sparrows, and males, respectively.

To our knowledge, there is currently no method to assess model fit for the Pradel method. Therefore, to assess fit, we estimated ϕ with the Cormack-Jolly-Seber method (CJS; Lebreton et al. 1992) in Program MARK, and tested goodness of fit (GOF) for the breeders, on plot set with Program RELEASE (Burnham et al. 1987).

Objective 2: Sensitivity of ϕ and f to nonbreeders.—The "all adults, on plot" set was used to quantify ϕ and f of all adults banded over the course of the study. "Breeders, on plot" (Objective 1) included 85.4% of the marked individuals; the additional 14.6% of individuals may have been migrants, floaters, adults whose nests failed before we detected their association, or nonbreeders (for sample sizes see Appendix). These individuals, referred to as "nonbreeders," were captured and resighted only in a single year and were never associated socially with a nest. This analysis included the same candidate model set ($n = 50$ models) and the same constraints for P as used in Objective 1.

Objective 3: Sensitivity of ϕ to local-scale dispersal.—To address the effects of local dispersal (1.5 km radius from the treatment fields) on survival, we added the 2005 and 2006 data collected during off-study field searches to capture histories within subsets of the "all adults, on plot" and "breeders, on plot" sets. These subsets excluded New York data, as off-site searches were conducted in Vermont only (Table 1; see Appendix 1 for sample sizes).

To assess ϕ, we used the Cormack-Jolly-Seber method (Lebreton et al. 1992) in Program MARK, and Program RELEASE to evaluate GOF. With treatment, species, and sex, the candidate model set included all combinations of two-way additive, two-way interactive, and three-way additive model ($n = 8$). Because recruitment should not be affected by the inclusion of emigrants from our study sites, f was not included in the model set, decreasing the number of models from those used in Objectives 1 and 2. Our data could not support a three-way interactive model.

Recapture–resight probabilities included data gathered only in Vermont and search effort varied among years. Here, P was a function of nest search effort (nest search vs. no nest search) and year (off-site observations vs. no off-site observations).

Objective 4: Finite rate of increase (λ, realized lambda) for the four treatments.—To understand source–sink dynamics in the Champlain Valley, we assessed the populations' finite rate of increase for each of the four treatment types. Realized lambda (λ), the observed growth rate of the population between sampling occasions, can be estimated with survival and recruitment values, $\lambda = \phi + f$ (Pradel 1996, Cooch and White 2007). Although this method provides an estimate of λ, we could not identify the relative contributions of death and emigration to the estimate of ϕ, nor the relative contributions of births vs. immigration to the estimate of f. Here, over the course of the study, $\lambda > 1$ indicated that the population size increased, $\lambda < 1$ indicated the population size decreased, and $\lambda = 1$ indicated the population size was stable. Males and females had 12 estimates of λ for each treatment, including all combinations of the two recruitment estimates and six

apparent survival estimates derived from Objectives 1–3 (ϕ breeders, on plot + f breeders, on plot; ϕ breeders, on plot + f all adults, on plot, etc.) As such, λ was presented as a 12-value range rather than our assessment of a best estimate. This objective, therefore, assessed which treatment-defined habitat types allowed population persistence for each species × sex combination.

RESULTS

Objective 1: Apparent survival and recruitment of known breeders

Breeders, on plot included capture histories for 725 Savannah Sparrows and 519 Bobolinks. The top-ranked model, $\phi_{\text{trt+spec+sex}} f_{\text{trt+spec+sex}}$ ($\omega_i = 0.76$; abbreviatiosn are trt, treatment; spec, species; Table 2), had six times more weight of support than the second-ranked model, $\phi_{\text{trt+spec+sex}} f_{\text{trt}\times\text{spec}}$ ($\omega_i = 0.11$), and 13 times more weight of support than the third-ranked model, $\phi_{\text{trt}\times\text{spec}} f_{\text{trt}\times\text{spec}}$ ($\omega_i = 0.06$). The observed field data fit the CJS modeling framework ($\chi^2 = 21.35$, df = 16, $P = 0.17$).

Savannah Sparrow ϕ.—Model-averaged survival estimates for male Savannah Sparrows ranged from 0.64 ± 0.09 on early-hayed to 0.78 ± 0.03 on late-hayed fields (Fig. 1A). Female survival rates were lower than for males and ranged from 0.48 ± 0.11 on early-hayed to 0.65 ± 0.07 on late-hayed fields. Overall, ϕ on late-hayed fields was notably higher than for all other treatments; in general, ϕ increased with decreasing management intensity for both sexes ($\phi_{\text{LH}} > \phi_{\text{MH}} > \phi_{\text{RG}} > \phi_{\text{EH}}$).

Bobolink ϕ.—Survival rates for Bobolinks were lower than for Savannah Sparrows in all treatments and for both sexes. Model-averaged estimates for male Bobolinks ranged from 0.43 ± 0.11 on early-hayed fields to 0.63 ± 0.08 on late-hayed fields (Fig. 1B). Female rates were lower than for males, ranging from 0.27 ± 0.09 on early-hayed fields to 0.46 ± 0.11 on late-hayed fields. As with Savannah Sparrows, survival increased with decreasing management intensity.

Savannah Sparrow f.—Recruitment was higher in early-hayed, middle-hayed, and grazed fields than in late-hayed fields. Model-averaged recruitment estimates for male Savannah Sparrows ranged from 0.20 ± 0.02 on late-hayed fields to 0.26 ± 0.05 to 0.27 ± 0.05 on the remaining fields (Fig. 2A). Female f was higher than male f and ranged from 0.24 ± 0.03 on late-hayed fields to 0.31 ± 0.06 to 0.32 ± 0.07 on the remaining fields.

Bobolink f.—Across all treatments, recruitment estimates were higher for Bobolinks than for Savannah Sparrows. Model-averaged recruitment estimates for male Bobolinks ranged from 0.25 ± 0.04 on late-hayed fields to 0.36 ± 0.09 on middle-hayed fields (Fig. 2B). Female recruitment rates were higher than for males and ranged from 0.30 ± 0.06 on late-hayed fields to 0.41 ± 0.11 on middle-hayed fields.

Objective 2: Sensitivity of ϕ and f to nonbreeders

The set of all adults, on plot included capture histories for 850 Savannah Sparrows and 606 Bobolinks. The

TABLE 2. All candidate models with $\Delta\text{AIC}_c < 10$ for "breeders, on plot" and "all adults, on plot" apparent survival (ϕ) and recruitment (f) analyses, with AIC_c weights (ω_i), Champlain Valley, USA, 2002–2006.

Data set and model	ΔAIC_c	$\text{AIC}_c \ \omega_i$	No. parameters
Breeders, on plot			
$\phi_{\text{trt+spec+sex}} f_{\text{trt+spec+sex}}$	0.000	0.764	17
$\phi_{\text{trt+spec+sex}} f_{\text{trt}\times\text{spec}}$	3.777	0.116	19
$\phi_{\text{trt}\times\text{spec}} f_{\text{trt}\times\text{spec}}$	5.130	0.059	21
$\phi_{\text{trt+spec+sex}} f_{\text{trt+sex}}$	7.961	0.014	16
$\phi_{\text{trt}\times\text{spec}} f_{\text{trt+spec}}$	8.312	0.012	18
$\phi_{\text{trt+spec+sex}} f_{\text{spec}\times\text{sex}}$	8.672	0.010	15
$\phi_{\text{trt+spec+sex}} f_{\text{trt+spec}}$	8.893	0.009	16
$\phi_{\text{trt}\times\text{spec}} f_{\text{trt+spec+sex}}$	9.529	0.007	19
All adults, on plot			
$\phi_{\text{trt}\times\text{spec}} f_{\text{trt}\times\text{spec}}$	0.000	0.860	21
$\phi_{\text{trt}\times\text{spec}} f_{\text{trt+spec}}$	4.765	0.079	18
$\phi_{\text{trt}\times\text{spec}} f_{\text{trt+spec+sex}}$	5.430	0.057	19

Notes: Model factors include four grassland treatments (early-hayed, middle-hayed, late-hayed, grazed), two species (Savannah Sparrow, Bobolink), and both sexes. Abbreviations are: trt, treatment; and spec, species.

top-ranked model, $\phi_{\text{trt}\times\text{spec}} f_{\text{trt}\times\text{spec}}$, had 11 times more weight of support ($\omega_i = 0.86$; Table 2) than the second-ranked model, $\phi_{\text{trt}\times\text{spec}} f_{\text{trt+spec}}$ ($\omega_i = 0.08$). In comparison to estimates for breeders, on plot, nonbreeders caused ϕ to decline and f to increase in 12 of 16 comparisons (Fig. 1A, B).

Savannah Sparrow ϕ.—Model-averaged survival estimates for male and female Savannah Sparrows ranged from 0.52 ± 0.10 on middle-hayed fields to 0.58 ± 0.09 to 0.59 ± 0.10 on remaining treatments. Thus, the inclusion of nonbreeders decreased male apparent survival estimates by 0.08 to 0.20 (−10% to −26%). Female estimates were 0.04 to 0.07 (−5% to −7%) lower on the middle- and late-hayed fields, and 0.05 to 0.10 higher (6% to 10%) on the early-hayed and grazed fields. The effects of management intensity and sex also decreased with the inclusion of additional adults in the data set (Fig. 1A).

Bobolink ϕ.—As with Savannah Sparrows, the inclusion of nonbreeders decreased survival estimates for male Bobolinks by 0.08 to 0.24 (−13% to −55%). However, unlike Savannah Sparrows, female Bobolink ϕ decreased on more intensively managed fields (by −0.08 for early-hayed and −0.06 for grazed), showed little change on moderately managed fields (0.03: middle-hayed), but increased on less intensively managed fields (by 0.08 for late-hayed). Thus, for Bobolinks, the effect of grassland habitat management on ϕ was magnified with the inclusion of potential nonbreeding adults (Fig. 1B).

Savannah Sparrow f.—For male Savannah Sparrows, f increased by 0.05 to 0.07 (18% to 21%) with the inclusion of nonbreeders, except on middle-hayed fields, where recruitment decreased by 0.03 (−11%; Fig. 2A). Female f estimates were relatively unchanged, with the exception of middle-hayed fields, where f decreased by 0.08 (−33%).
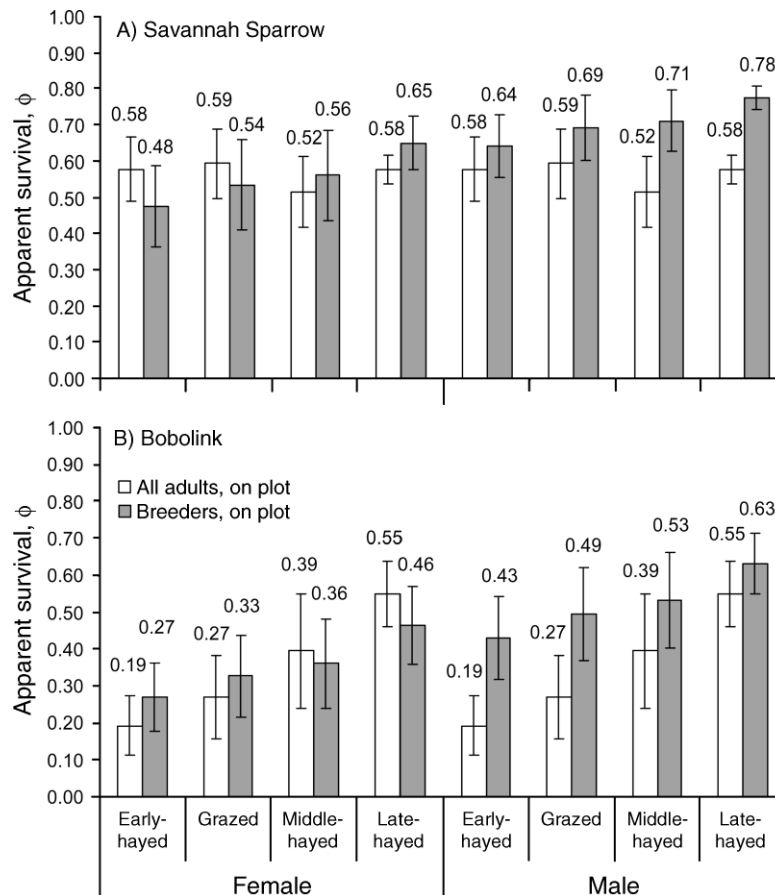
FIG. 1. (A) Savannah Sparrow (*Passerculus sandwichensis*) and (B) Bobolink (*Dolichonyx oryzivorus*) apparent survival (ϕ) in relation to grassland management. The four treatments are ordered by management intensity, from highest intensity (early-hayed) to lowest intensity (late-hayed). Error bars indicate $\pm$SE.

Bobolink f.—The addition of nonbreeders in Bobolink recruitment estimates generally had the same effect as on Savannah Sparrow estimates: recruitment increased for males and stayed the same for females (Fig. 2B).

Objective 3: Sensitivity of ϕ to local-scale dispersal

To assess the sensitivity of ϕ to the inclusion of birds dispersing outside the study fields, we compared Cormack-Jolly-Seber model-averaged estimates derived from four data sets, all collected in Vermont: (1) breeders, with dispersers, (2) breeders, no dispersers, (3) all adults, with dispersers, and (4) all adults, no dispersers (Fig. 3A, B). In data sets 1–3, model $\phi_{trt+spec+sex}$ had >90% of the model weights (Table 3), and ranked second in set 4 ($\omega_i = 0.17$).

Savannah Sparrows.—For male Savannah Sparrows in all treatments, local-dispersal data increased estimates of ϕ, as well as estimate precision. Male survival rates were highest for "breeders, with dispersers" and lowest for "all adults, no dispersers." In general, estimates of ϕ were notably higher for males on less intensively managed fields (late-hayed) than on moderate (middle-hayed) and intensively (early-hayed, grazed) managed

fields. Females showed a similar pattern with respect to grassland management effects on ϕ; however, within each treatment, females showed less variation among the four data sets than males (Fig. 3A).

Bobolinks.—As with Savannah Sparrows, the inclusion of off-site dispersers increased survival estimates for male Bobolinks in all treatments. These effects were especially strong on intensively managed fields (early-hayed, grazed) using the two all adults data sets (Fig. 3B). Unlike male ϕ, female Bobolink ϕ showed little variation across intensively and moderately managed fields, regardless of which of the four data sets were analyzed.

Objective 4: Finite rate of increase (λ, realized lambda) for the four treatments

With results from Objectives 1–3, we generated 12 estimates of lambda for each species, treatment, and sex. The amount of variation among lambda estimates differed among species, treatments, and sexes (Fig. 4). Males of both species showed greater variation among λ estimates than did females. Only male Savannah Sparrows in all treatments showed potential population
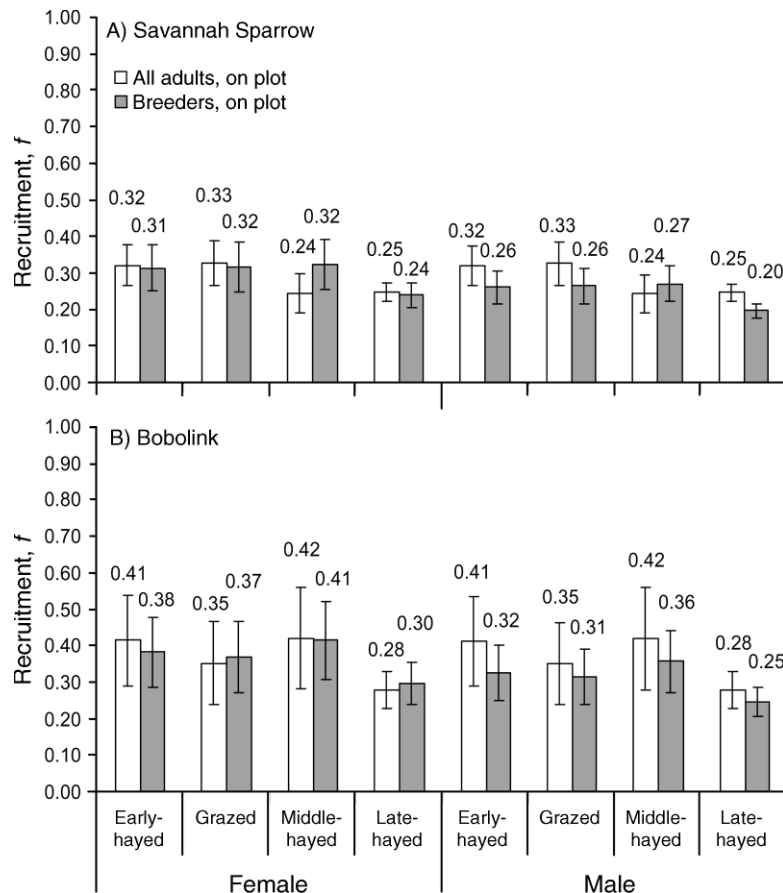
FIG. 2. (A) Savannah Sparrow and (B) Bobolink recruitment (f) increased with grassland management intensity. The four treatments are ordered by management intensity, from highest intensity (early-hayed) to lowest intensity (late-hayed). Each individual included in "breeders, on plot" had a known breeding history for at least one year on one of nine treatment fields; with 14.6% more capture histories; "all adults, on plot" included all individuals banded on treatment fields, including potential nonbreeders. Error bars indicate ±SE.

increases within the sampling period. Ranges with maximum values for male Savannah Sparrows included late-hayed ($\lambda = 1.10–0.80$) and grazed fields ($\lambda = 1.08–0.86$). All estimates for female Savannah Sparrows were <1.0, with highest estimates again on late-hayed ($\lambda = 0.96–0.82$) and grazed fields ($\lambda = 0.92–0.83$). For male Bobolinks, highest estimates were also on late-hayed ($\lambda = 0.98–0.81$) and middle-hayed fields ($\lambda = 0.97–0.74$). Female Bobolinks showed the overall greatest rates of population decline; λ estimates were highest on late-hayed ($\lambda = 0.84–0.74$) and middle-hayed fields ($\lambda = 0.81–0.73$).

DISCUSSION

The results for Objective 1 showed that birds breeding in less intensively managed grasslands achieved higher apparent survival than those breeding in intensively managed grasslands. Management-mediated decreases in ϕ resulted from either increased mortality or failure to return to the study area. Survival was greater for males than females and greater for Savannah Sparrows than

Bobolinks. Birds using late-hayed fields had >25% higher apparent survival than those on more intensively managed early-hayed, middle-hayed, and grazed fields; male apparent survival was 35% higher than female apparent survival; Savannah Sparrow apparent survival was 44% higher than Bobolink apparent survival.

Recruitment was highest on both intensively and moderately managed fields, perhaps as a result of lower apparent survival on these fields. Higher recruitment and lower survival on intensively managed fields indicates greater population turnover relative to less intensively managed fields. Compared to late-hayed fields, populations on intensively or moderately managed fields included 33–34% more individuals who entered the system through birth or emigration for each surviving adult. Because intensively managed fields have little productivity, populations are dependent on receiving immigrants. Bobolink recruitment was 23% greater than Savannah Sparrow recruitment. Contrary to the survival trends, recruitment was consistent between sexes of a given species. Together, the survival and
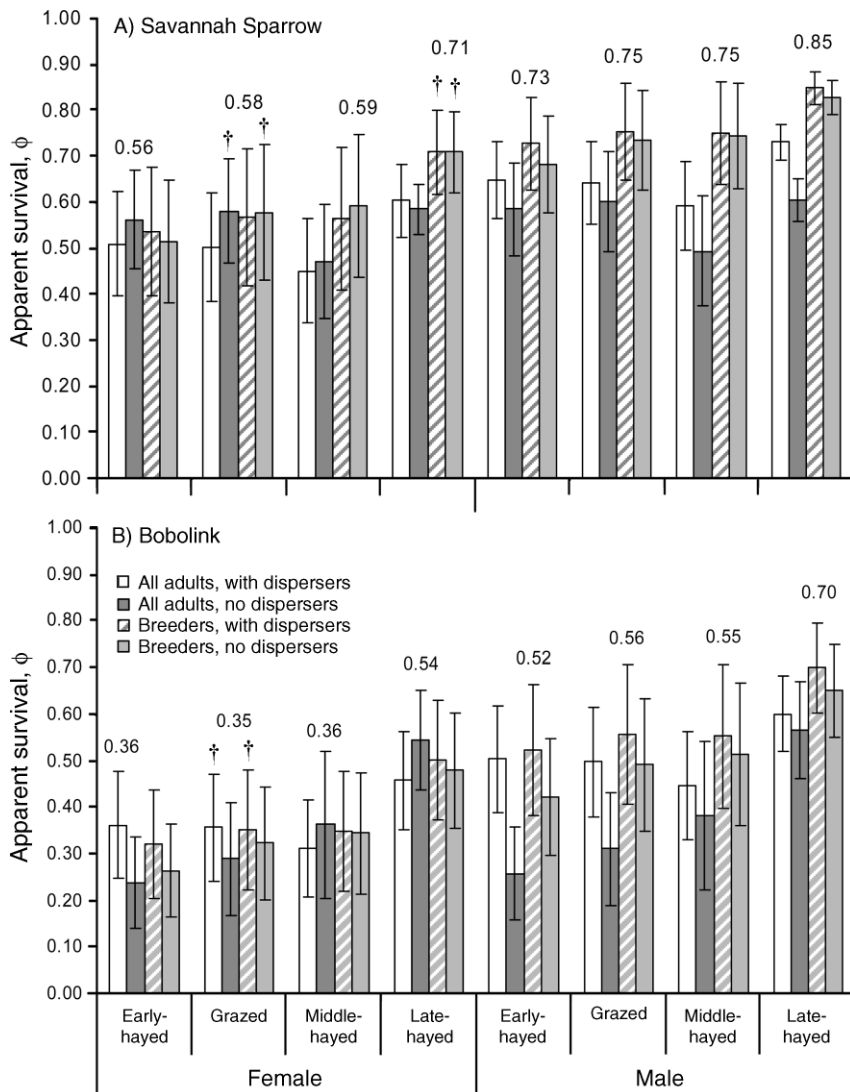
Fig. 3. (A) Savannah Sparrow and (B) Bobolink apparent survival estimates (ϕ) in relation to breeding status and search area. For males, survival estimates and precision increased with dispersal searches of <1.5 km from study fields; female estimates responded only within certain grassland treatments, and this response varied between species. The four treatments are ordered by management intensity, from highest intensity (early-hayed) to lowest intensity (late-hayed). Displayed values are the highest apparent survival estimate; daggers indicate that the greatest value was equal between two estimates; error bars indicate ±SE.

TABLE 3. Including only data from the Vermont study fields, candidate models exploring the effects of local dispersal (<1.5 km from study fields) on apparent survival (ϕ) estimates show overwhelming support for model $\phi_{trt+spec+sex}$.

Model	No. parameters	All adults, no dispersers		All adults, with dispersers		Breeders, no dispersers		Breeders, with dispersers	
		ΔAIC_c	$AIC_c\ \omega_i$	ΔAIC_c	$AIC_c\ \omega_i$	ΔAIC_c	$AIC_c\ \omega_i$	ΔAIC_c	$AIC_c\ \omega_i$
$\phi_{trt+spec+sex}$	9	3.085	0.175	0	0.904	0	0.941	0	0.989
$\phi_{trt+spec}$	8	13.975	0.001	15.987	0	21.916	0	27.946	0
$\phi_{trt+sex}$	8	27.616	0	14.59	0.001	36.719	0	26.784	0
$\phi_{trt \times spec}$	11	0	0.818	10.393	0.005	5.575	0.058	19.368	0
$\phi_{trt \times sex}$	11	27.613	0	13.602	0.001	36.452	0	26.657	0
$\phi_{spec+sex}$	6	10.28	0.005	5.275	0.065	13.726	0.001	9.732	0.008
$\phi_{spec \times sex}$	7	12.103	0.002	7.255	0.024	15.752	0	11.56	0.003
ϕ	4	45.853	0	37.56	0	67.948	0	62.392	0

Note: Model factors include four grassland treatments (early-hayed, middle-hayed, late-hayed, grazed), two species (Savannah Sparrow, Bobolink), and both sexes.
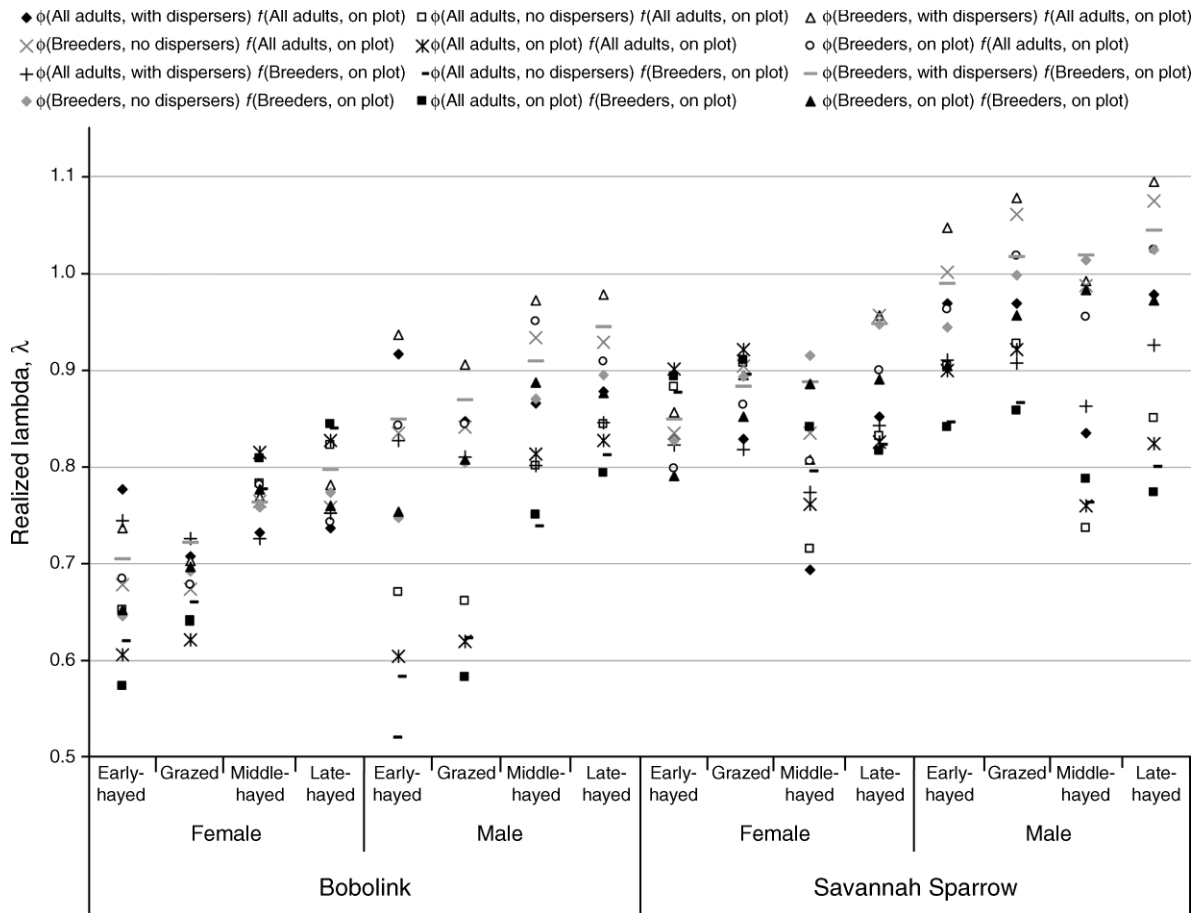
◆ φ(All adults, with dispersers) *f*(All adults, on plot) □ φ(All adults, no dispersers) *f*(All adults, on plot) △ φ(Breeders, with dispersers) *f*(All adults, on plot)

✕ φ(Breeders, no dispersers) *f*(All adults, on plot) ✶ φ(All adults, on plot) *f*(All adults, on plot) ○ φ(Breeders, on plot) *f*(All adults, on plot)

+ φ(All adults, with dispersers) *f*(Breeders, on plot) − φ(All adults, no dispersers) *f*(Breeders, on plot) − φ(Breeders, with dispersers) *f*(Breeders, on plot)

◆ φ(Breeders, no dispersers) *f*(Breeders, on plot) ■ φ(All adults, on plot) *f*(Breeders, on plot) ▲ φ(Breeders, on plot) *f*(Breeders, on plot)

FIG. 4. Variation in realized lambda ($\lambda = \phi + f$) estimates for Savannah Sparrows and Bobolinks breeding in four grassland treatment types of the Champlain Valley, Vermont and New York, USA. Variation spans 12 estimates comprising all combinations of two recruitment estimates and six apparent survival estimates from Objectives 1–3.

recruitment patterns suggest that if annual productivity results in a balanced sex ratio, through death and emigration, this population of Bobolinks, and to a lesser extent Savannah Sparrows, may be male biased.

Our results provide strong evidence for the importance of knowing the breeding status of individuals when conducting demographic analyses. The presence of nonbreeders significantly decreased apparent survival estimates and increased recruitment estimates for these species (Objective 2). For males of both species, the presence of nonbreeders decreased the precision of, and lowered, apparent survival estimates by ~25%. Differing by ~1%, female estimates of φ showed little variation with inclusion of nonbreeders, suggesting that female settlement decisions are made quickly, and once settled, females attempt to breed. Like φ, female recruitment estimates were largely unchanged by potential nonbreeders. Although large sample sizes are critical for survival analyses, results may be compromised by including a large proportion of nonbreeders that may be substantially more nomadic than those tied to a breeding site.

Local dispersal data increased apparent survival estimates and, in many cases, increased precision, although the effect was stronger for Savannah Sparrows than Bobolinks, and for males than females (Objective 3). Although we attempted to detect both males and females, these results may be slightly male biased, as females in the incubation stage, especially Savannah Sparrows, were inconspicuous. Nonetheless, these results provide an important contrast to the only comparable study that explored the role of local dispersal in estimating apparent survival. Using search radii similar to this study, Cilimburg et al. (2002) found that local dispersal data increased φ in the Yellow Warbler (*Dendroica petechia*) from 0.42 to 0.49 for males and from 0.35 to 0.41 for females. In some cases, the effect of including dispersal data was greater in our study. Male Savannah Sparrow and Bobolink φ in late-hayed fields increased from 0.60 to 0.85 and 0.57 to 0.70, respectively. Effect sizes were more than three times that observed by Cilimburg et al. (2002). Data from off-field searches showed greater between-year dispersal distances for Bobolinks relative to Savannah Sparrows (N.

Fajardo, A. Strong, and N. Perlut, *unpublished data*), consistent with the effects on apparent survival noted in the *Discussion*.

Dispersal data complicated the interpretation of estimates of female ϕ on the intensively and moderately managed fields. Dispersal observations increased survival estimates for female Bobolinks on early-hayed and grazed fields, but did not affect survival estimates for female Savannah Sparrows. Paired with nesting observations, these results make intuitive sense. Bobolinks abandoned early-hayed fields immediately after haying, and Savannah Sparrows remained and immediately renested (Perlut et al. 2006). Therefore, during post-haying dispersal, Bobolinks may assess local breeding habitats for opportunities in both current and future years as 19% to 32% of hayfield habitat is harvested for forage prior to 11 June. This behavior is potentially an ecologically "good" decision, as reproductive success on early-hayed fields is near zero, and is low on pastures (Perlut et al. 2006). Alternatively, local dispersal had little to no effect on survival estimates for middle- and late-hayed fields, where Bobolinks were more philopatric and reproductive success was moderate to high, respectively.

As do the return rates from Bollinger and Gavin (1989), these results suggest that surviving females who select high-quality fields either return to their previous breeding site or disperse at a scale >1.5 km. Some males, however, appear to disperse locally regardless of previous years' habitat and reproductive success (N. Fajardo, A. Strong, and N. Perlut, *unpublished data*). This behavior may be a product of a polygynous social mating system, where males with the highest quality territories monopolize up to three social mates (N. Perlut, *unpublished data*), leaving some males with no social mates. For females, large-scale dispersal could also be mediated by the polygynous social mating system, where males bear the cost of territory establishment and defense, and females select among males based on resources (Greenwood 1980). Females whose nests fail (especially as a result of haying) may have weak bonds to the given location, and potentially disperse in search of higher quality territories. However, females on late-hayed fields are equally likely to return to the previous year's location regardless of nest success (N. Fajardo, A. Strong, and N. Perlut, *unpublished data*). Therefore, we suspect that dispersal >1.5 km may be a joint effect of individual nest failure, population (field level) nest failure, and dramatic habitat alteration (cutting and removal of grass).

Although the effects of both nonbreeders and local dispersal on apparent survival estimates are notable, as evidenced in lambda ranges, Bobolinks paid a significant cost in survival when they selected fields that were hayed or grazed during the breeding season. Along with low productivity, treatment-specific survival costs are likely limiting the population, as high recruitment rates (here, primarily immigration) were unable to offset low

survival rates to maintain stable populations. Some portion of adults likely emigrate further than our dispersal effort could detect (A. Strong, *unpublished data*); however, it is unlikely that this group would be large enough to increase apparent survival estimates to the level achieved in late-hayed fields. For example, in a concurrent breeding dispersal study, nearly 90% and 93% of detected Bobolinks and Savannah Sparrows, respectively, returned to their previous field regardless of nest success in the previous year or available habitat within 1.5 km (N. Fajardo, *unpublished data*). Therefore, we expect that the number of individuals dispersing >1.5km to be >0, though small enough such that, if all individuals were detected, survival estimates would not equal those observed on late-hayed fields.

Migration and wintering constraints affect survival, though these processes likely exert similar effects on the entire population regardless of the treatment type in which individuals breed. As such, two breeding-ground scenarios may account for the increased mortality on intensively managed fields: (1) haying-mediated, within-season dispersal may increase predation risk; and (2) haying-mediated, within-season dispersal may limit access to resources when preparing for migration. In both cases, within-season dispersal increases mortality rates. Birds on intensively managed fields can disperse to less intensively managed fields, which likely increases productivity; however, potential gains in productivity come at the expense of decreased ϕ. Given low Bobolink λ estimates, within-season movement likely results in little added productivity. Interestingly, these results appear contrary to Fletcher et al. (2006), whose population growth models for Bobolinks breeding in restored grassland in Iowa, USA, suggested that factors during the nonbreeding season affected ϕ more than those during the breeding season. This may be a result of the wide variation in management intensities encompassed in this study.

Grassland management also strongly affected recruitment. First-time breeders and new emigrants settled more frequently in low- (early-hayed and grazed) or moderate-quality fields (middle-hayed) than in high-quality fields (late-hayed). Though this study was not designed to identify the mechanism driving recruitment, two factors may contribute. First, breeders in late-hayed fields have high survival and philopatry; therefore, these fields are likely at a density-dependent carrying capacity and offer fewer free territories each year (Pulliam and Danielson 1991), particularly for males. Here, increased survivorship comes with the benefit of high productivity; however, despotic behavior comes with the cost of denying your progeny high-quality breeding sites. Alternatively, upon spring arrival, the rapid plant growth on early-hayed, middle-hayed, and grazed fields may be more attractive to novice individuals when making settlement decisions. Grass is removed from these fields in the autumn, thereby promoting a "greener" spring appearance which may imitate co-

evolved cues that otherwise suggest high habitat quality (Robertson and Hutto 2006). In this scenario, populations are limited by density-dependent territory vacancies created in more intensively managed fields. However, in the Champlain Valley, for surviving breeders from late-hayed fields, habitat structural cues are less important than knowledge of past breeding success, as they clearly chose to return to late-hayed fields rather than select these other habitats. In a less intensively managed study system, Bobolinks used the number of young produced as "public information" to assess field quality (Nocera et al. 2005); a trend that appears true for experienced breeders in this population, but not for novice breeders.

These results strongly suggest that Bobolinks and, to a lesser extent, Savannah Sparrows, illustrate classic source–sink dynamics within the mosaic of treatment-defined grassland habitat types in the Champlain Valley. High-quality habitats produce more offspring, and adults that maintain territories on these fields both survive longer and have higher field-level philopatry than do individuals from low-quality habitats. Treatment-specific ranges for λ show that populations may be close to stable on late-hayed fields, and significantly declining on the other three treatments. Reproductive data show that late- and middle-hayed fields also produce offspring at a rate higher than female–female replacement (Perlut et al. 2006). Of critical management and long-term population interest, though, is how these data apply to the behavioral characteristic that separates a source–sink system from an ecological trap. In both a sink and a trap, habitat characteristics result in low productivity; however, in a trap, individuals show preference for low-quality habitats. Here we show that individuals entering the system through birth and immigration disproportionately select low-quality over high-quality fields. These data, along with the fact that both species initiate nesting activities earlier on low-quality fields (Perlut et al. 2006), may indicate preference (Robertson and Hutto 2006) for low-quality fields, and be evidence that intensively managed fields are ecological traps.

Bobolinks, with low adult survival, attraction to fields with low productivity, and a landscape increasingly devoted to intensive management (Perlut et al. 2006), illustrate the need for serious conservation management. Although the effects are less strong for Savannah Sparrows, conservation measures that improve habitat quality will support both species. To further understand processes regulating the Champlain Valley's grassland songbirds, the next step is to apply survival and productivity parameters to the relative proportion of the dominant habitat types. Understanding the landscape-level characteristics of grassland management will allow us to use these life-history parameters to model habitat requirements that would stabilize populations before these species face endangerment.

LITERATURE CITED

Adams, A. A. Y., S. K. Skagen, and J. A. Savidge. 2006. Modeling post-fledging survival of Lark Buntings in response to ecological and biological factors. Ecology 87:178–188.

Anders, A. D., and M. R. Marshall. 2005. Increasing the accuracy of productivity and survival estimates in assessing landbird population status. Conservation Biology 19:66–74.

Bedard, J., and G. LaPointe. 1984. Banding returns, arrival times, and site fidelity in the Savannah Sparrow. Wilson Bulletin 96:196–205.

Bedard, J., and G. LaPointe. 1985. Influence of parental age and season on Savannah Sparrow reproductive success. Condor 87:106–110.

Bollinger, E. K., P. B. Bollinger, and T. A. Gavin. 1990. Effects of hay-cropping of eastern populations of the Bobolink. Wildlife Society Bulletin 18:143–150.

Bollinger, E. K., and T. A. Gavin. 1989. The effects of site quality on breeding-site fidelity in Bobolinks. Auk 106:584–594.

Brennan, L. A., and W. P. Kuvlesky. 2005. North American grassland birds: An unfolding conservation crisis? Journal of Wildlife Management 69:1–13.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference, second edition. Springer, New York, New York, USA.

Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release–recapture. American Fisheries Society, Bethesda, Maryland, USA.

Cilimburg, A. B., M. S. Linderberg, J. J. Tewksbury, and S. J. Hejl. 2002. Effects of dispersal on survival probabilities of adult Yellow Warblers (Dendroica Petechia). Auk 119:778–789.

Cooch, E. G., and G. C. White. 2007. Program MARK A gentle introduction. Fifth edition. ⟨http://www.phidot.org/software/mark/docs/book/⟩

Crouse, D. T., L. B. Crowder, and H. Caswell. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology 68:1412–1423.

Donovan, T. M., F. R. Thompson III, J. Faaborg, and J. R. Probst. 1995. Reproductive success of migratory birds in habitat sources and sinks. Conservation Biology 9:1380–1395.

Fletcher, R. J., R. R. Koford, and D. A. Seaman. 2006. Critical demographic parameters for declining songbirds breeding in restored grasslands. Journal of Wildlife Management 70:145–157.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behavior 28:1140–1162.

Hagen, C. A., J. C. Pitman, B. K. Sandercock, R. J. Robel, and R. D. Applegate. 2005. Age-specific variation in apparent survival rates of male Lesser Prairie-Chickens. Condor 107:78–86.

Hannah, L., J. L. Carr, and A. Lankerani. 1995. Human disturbance and natural habitat: a biome level analysis of a global data set. Biodiversity and Conservation 4:128–155.

Kershner, E. L., J. W. Walk, and R. E. Warner. 2004a. Breeding-season decisions, renesting, and annual fecundity of female Eastern Meadowlarks (Sturnella magna) in Southeastern Illinois. Auk 121:796–805.

Kershner, E. L., J. W. Walk, and R. E. Warner. 2004b. Postfledging movements and survival of juvenile Eastern Meadowlarks (Sturnella magna) in Illinois. Auk 121:1146–1154.

Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67–118.

Murphy, M. T. 2003. Avian population trends within the evolving agricultural landscape of Eastern and Central United States. Auk 120:20–34.

Nocera, J. J., G. J. Forbes, and L. A. Giraldeau. 2005. Inadvertent social information in breeding site selection of natal dispersing birds. Proceedings of the Royal Society B 273:349–355.

Perkins, D. W., P. D. Vickery, and W. G. Shriver. 2003. Spatial dynamics of source-sink habitats: Effects on rare grassland birds. Journal of Wildlife Management 67:588–599.

Perlut, N. G. 2007. Effects of hayfield management on grassland songbirds: behavioral responses and population processes. Dissertation. University of Vermont, Burlington, Vermont, USA.

Perlut, N. G., A. M. Strong, T. M. Donovan, and N. J. Buckley. 2006. Grassland songbirds in a dynamic management landscape: behavioral responses and management strategies. Ecological Applications 16:2235–2247.

Peterjohn, B. G., and J. R. Sauer. 1999. Population status of North American grassland birds from the North American breeding bird survey, 1966–1996. Studies in Avian Biology 19:27–44.

Pradel, R. 1996. Utilization of mark–recapture for the study of recruitment and population growth. Biometrics 52:703–709.

Pradel, R., J. E. Hines, J. D. Lebreton, and J. D. Nichols. 1997. Capture–recapture survival models taking account of transients. Biometrics 53:60–72.

Pulliam, H. R. 1988. Sources, sinks, and population regulations. American Naturalist 132:652–661.

Pulliam, H. R., and B. J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population-dynamics. American Naturalist 137:S50–S66.

Robertson, G. A., and R. L. Hutto. 2006. A framework for understanding ecological traps and an evaluation of existing evidence. Ecology 87:1075–1085.

Sauer, J. R., J. E. Hines, and J. Fallon. 2005. The North American breeding bird survey. Results and analysis 1966–2004. Version 2005.2. USGS Patuxent Wildlife Research Center, Laurel, Maryland, USA.

Shustack, D. P. 2004. Bobolink and savannah sparrow habitat selection in the Champlain Valley. Thesis. University of Vermont, Burlington, Vermont, USA.

Troy, A. R., A. M. Strong, S. C. Bosworth, T. M. Donovan, N. J. Buckley, and J. L. Wilson. 2005. Attitudes of Vermont dairy farmers regarding adoption of management practices for grassland songbirds. Wildlife Society Bulletin 33:528–538.

Walk, J. W., K. Wentworth, E. L. Kershner, E. K. Bollinger, and R. E. Warner. 2004. Renesting decisions and annual fecundity of female Dickcissels (Spiza americana) in Illinois. Auk 121:1250–1261.

Warner, R. E., and S. L. Etter. 1989. Hay cutting and the survival of pheasants: a long-term perspective. Journal of Wildlife Management 53:455–461.

Wheelwright, N. T., and R. A. Mauck. 1998. Philopatry, natal dispersal, and inbreeding avoidance in an island population of Savannah Sparrows. Ecology 79:755–767.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:S120–S139.

APPENDIX

Sample sizes for apparent survival and recruitment analyses, including individuals banded in 2002–2005, and resight–recaptured in 2003–2006 in the Champlain Valley of Vermont and New York, USA (*Ecological Archives* E089-113-A1).